What faecal pellet surveys can and can't reveal about the ecology of koalas *Phascolarctos cinereus*

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ABSTRACT

Previous approaches to indirect detection of koala presence have been proposed, however, the present paper identifies issues of bias, pellet detectability and over-analysis of information inherent in those prior techniques. We recommend an approach that reduces bias, can be consistently applied and enables information on presence of koalas *Phascolarctos cinereus* to be used to inform larger survey programs, 'ground-truth' predictive habitat mapping, etc. We describe a rapid assessment methodology based on indirect signs that provides a reproducible, statistically valid, time-efficient and resource-efficient protocol for determining the presence of this species. The application, advantages and limitations of this 'koala rapid assessment method' (KRAM) are discussed with reference to its role in the design of detailed and landscape scale *P. cinereus* surveys.

Key words: Bias, survey design, koalas, stratification, absence, random sampling

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Introduction

Highly-publicised declines in koala *Phascolarctos cinereus* populations through much of the species' range have intensified scientific and public interest in protecting this internationally iconic animal (Senate 2011). Conservation efforts for any given species need to be informed by an evidence based understanding of its distribution and abundance. In the case of this cryptic, often-sparsely distributed species, resource and time-intensive field studies are ultimately required. Evidence accepted by the Australian Senate's recent *Inquiry into the status, health and sustainability of Australia's koala population* emphasised the lack of basic population trend data from many parts of the species' range, though robust data are available from particular study locations (Senate 2011)[1].

There is a substantial literature on the use of faecal deposition to estimate various species' habitat occupancy and abundance (e.g. Johnson and Jarman 1987, Hiby and Lovell 1991, Jachmann 1991, Barnes 1993). However, Caughley (1993) has raised the issue that preliminary studies that would enable better targeted surveys are often absent from large-scale investigations. Our approach provides an opportunity to acquire information about the distribution of the study species in order to assist in targeting subsequent, more detailed surveys, as well as being useful in the context of environmental impact studies and validation of habitat modelling, etc.

In order to reduce fieldwork effort, faecal pellet surveys have been used to make inferences about *P. cinereus* biology / ecology. Although the methodological basis for such surveys has not been well established in the peer reviewed literature, the potential of such indirect survey approaches has attracted interest (Ellis et al. 1998, Phillips and Callaghan 2000, Sullivan et al. 2002, Phillips and

1. See Letter to Minister Burke at http://www.environment.gov.au/biodiversity/threatened/species/pubs/koala-tssc-letter.pdf and subsequent response to Senate at http://www.senate.aph.gov.au/submissions/comittees/viewdocument.aspx?id=c277bb05-6999-479f-914d-5366a5ba5e68 senate.aph.gov.au/submissions/comittees/viewdocument.aspx?id=c277bb05-6999-479f-914d-5366a5ba5e68

Callaghan 2011, Rhodes et al. 2011). Despite evidence of the limitations in the applicability of faecal pellet detection techniques, they continue to be promoted for use in determining habitat utilisation by *P. cinereus* and for identification of important habitat areas for protection and conservation (McAlpine et al. 2006, Phillips and Callaghan 2011). While searching for signs (rather than actual *P. cinereus* individuals) can provide time and resource efficiencies in understanding some aspects of *P. cinereus* biology, care must be taken not to over interpret data that are collected. For example, pellet deposition under trees has been purported by some authors to provide evidence of browse consumption, but has been clearly shown to be an unreliable indicator of diet or even tree preference (Ellis et al. 2002, Matthews et al. 2007). Estimating abundance from faecal pellet surveys requires prior knowledge of the relationship between pellet occurrence and actual *P. cinereus* density (Sullivan et al. 2002, Rhodes et al. 2011) that can only be acquired by calibration with direct surveys (observations).

There are fundamental problems in attempting to extrapolate faecal pellet surveys to generate abundance or density estimates; however, with the appropriate use and interpretation of data obtained from a robust, reproducible method for determining *P. cinereus* presence, studies of the species' biology would be better informed and more effective use of restricted resources could be achieved. For example, using indirect signs to identify parts of the landscape that should be targeted during large scale survey programs would reduce variability associated with estimating *P. cinereus* density and a rapid assessment protocol can permit a much more representative 'ground-truthing' of habitat predictions based on remote sensing and particular habitat attributes. Here we present details of a koala-optimised rapid assessment methodology (KRAM) based on indirect signs, that allows for the presence of *P. cinereus* to be determined in a consistent, unbiased, time-efficient and resource-efficient manner. The limitations of this methodology are also discussed.

Direct observation difficulties

As a result of the cryptic nature of the species and the typically low densities at which it occurs in the landscape, critical parameters of *P. cinereus* field biology such as density, abundance and dispersal are difficult to quantify (Sullivan et al. 2002, Dique et al. 2003). Various techniques have been used to sample wild *P. cinereus* populations, including daytime searches of strip transects with fixed boundaries (Dique et al. 2004), distance sampling along line-transects (Dique et al. 2003), mark-resight estimates (Hasegawa 1995) and spotlight surveys (Smith and Andrews 1997). While these and other studies have contributed important information about abundance of discrete *P. cinereus* populations, a major limitation is that they depend on direct observations, which are difficult to make in the wild. Recognised census techniques such as these often produce relatively low data yields in spite of intensive survey effort. This can be attributed to the usually sparse distribution of the species across the landscape (Sullivan et al. 2002).

In addition, any inferences drawn from direct observations of a sparsely distributed and cryptic animal are vulnerable to being strongly influenced by even a small number of missed observations (Sullivan et al. 2002). These underestimations may result from failure to detect an animal actually present within the habitat being sampled, or temporal variability in habitat utilisation. Low density populations are also vulnerable to temporal variability in habitat utilisation producing random increases in estimates (DERM 2012).

This vulnerability to missed observations or temporal variability may be overcome by intensifying sampling effort (spatial extent of area surveyed, number of sites surveyed, number of observers) in a given study area. However, in many instances, constraints associated with limited human and financial resources are likely to prevent such an increase in sampling intensity. And in some cases, for example when establishing or monitoring current distribution, information about the presence of the species may be all that is required.

The use of faecal pellets as indirect indicators – and more

Indirect signs can provide useful information. Indeed, faecal pellet searches have been an integral feature of field surveys in previously published *P. cinereus* studies, even though the underlying methodology was not published until recently (Phillips and Callaghan 2011). Lack of a peer reviewed methodology also has not inhibited the frequent incorporation of faecal pellet searches in (unpublished) environmental impact assessments associated with development applications and other 'grey literature'.

Faecal pellets from *P. cinereus* are readily identifiable, reasonably detectable and persist post-departure of the animal (Witt and Pahl 1995, Sullivan et al. 2002, Cristescu et al. 2011). These characteristics also apply to the distinctive scratch marks *P. cinereus* leave on smooth barked trees; but where the habitat is composed predominantly or exclusively of rough barked trees, faecal pellets provide the most effective means of indirect assessment. The relative ease of finding and identifying traces such as faecal pellets allows for the presence of *P. cinereus* to be confirmed without requiring more intensive searches for individual animals. Indirect traces allow for past as well as present habitat occupancy to be evaluated, in contrast to direct observations that rely on the target species being present in the sampled habitat at the time of survey (Rhodes et al. 2011). Searching for indirect traces such as faecal pellets requires little advanced training and involves minimal disturbance to animals or their habitat (Sullivan et al. 2002). A significant advantage of surveying for *P. cinereus* presence through detection of faecal pellets is that it allows for large areas to be assessed in a time-efficient manner (Sullivan et al. 2002, Sullivan et al. 2004).

Stratified random sampling has underpinned the selection of individual survey sites within the majority of discrete study areas in previously published *P. cinereus* assessments. Stratification has typically been based on landscape scale habitat features, for example: landform classes, vegetation communities, dominant soil types and rainfall zones (Sullivan et al. 2003b), mapped vegetation communities,

aspect and topography (Samedi 1995, Lunney et al. 2000) and geological units and vegetation communities (Phillips and Callaghan 2000, Phillips and Callaghan 2011). Where little or no existing information on *P. cinereus* distribution is available, particularly over large spatial scales, a preliminary investigation based upon a rapid assessment of faecal pellets may be useful by providing indications of *P. cinereus* distribution and thus can assist detailed survey / study design. For instance, Sullivan et al. (2003b) used a weighted sampling matrix based on identified rainfall zones to determine the number of transects assessed per sample. Survey site numbers per stratum were further dependent on the relative level of *P. cinereus* utilisation, as determined through preliminary surveys (Sullivan et al. 2003b).

As well as being used to assess presence / absence of *P. cinereus*, analyses of faecal pellets have been undertaken to study various other aspects of *P. cinereus* ecology, including tree species preference (Phillips 2000, Phillips and Callaghan 2000), abundance (Sullivan et al. 2004), broad-scale patterns of habitat use (Sullivan et al. 2003a) and dietary analysis (Ellis et al. 2002). It should be emphasised that in order to obtain valid determination of parameters other than *P. cinereus* presence, more is required than basic pellet counts. Modelling studies (see McAlpine et al. 2006, Rhodes et al. 2006a, Rhodes et al. 2006b, Januchowski et al. 2008) and *P. cinereus* habitat mapping (see Lunney et al. 2000) were predominantly desktop based assessments; but incorporation of faecal pellet surveys as a field validation component was found to be valuable.

Previous faecal pellet sampling protocols and some of their limitations

Techniques used to detect *P. cinereus* faecal pellets have varied between studies. The most common approach has been to employ some variation of the "spot assessment technique" (SAT) first referred to by Phillips and Callaghan (Phillips and Callaghan 2000, Phillips and Callaghan 2011).

A critical step of the SAT as described in Phillips and Callaghan (2011) suffers from a fundamental flaw due to a potential for bias in selecting the "focal trees" (as previously noted in Dique et al. 2004). A focal tree is selected on the basis of the following criteria:

"a. *a tree of any species beneath which one or more P. cinereus faecal pellets have been observed and/or*

b. *a tree in which a P. cinereus has been observed and/or*

c. *any other tree known or considered to be potentially important for P. cinereus, or of interest for other assessmsnt purposes*".

This step violates the requirement for randomness and thus jeopardises the whole method; statistical analysis generally relies upon randomness and minimisation of bias of the data. In any case it is quite unclear why the authors (Phillips and Callaghan 2011) thought it necessary to include this problematic feature, rather than simply commencing a survey at a randomly located tree. Moreover, one of the main principles of the scientific method is reproducibility of research, which refers to the ability of an entire experiment or study to be reproduced by someone else working independently. This encapsulates the concept that the ultimate product of research is a paper including the integral component of the full methodology and computational analysis necessary for reproduction of the results and building upon the research. Fundamental to the process is the requirement for the method to be independent of individuals and their idiosyncrasies – inherently the SAT is not reproducible because only the one observer can make the same sort of selection of the initial 'focal tree' and thus different observers are likely to arrive at different findings for the same site.

A second weakness is the "strict adherence to the 100 cm around the base of each tree". This focus on the base of the tree is recurrent in the literature. Searches within 1 m of the base of all trees within a 40 x 40 m quadrat were conducted by Phillips et al. (2000), Phillips and Callaghan (2000) and Phillips and Callaghan (2011). Individual searches involved a precursory inspection around the base of the focal tree, followed by a more comprehensive inspection, including disturbance of ground cover and leaf litter (Phillips et al. 2000, Phillips and Callaghan 2000). Sullivan et al. (2002) conducted faecal pellet searches within a 30 cm radius of the base of every eucalypt tree (diameter at breast height (dbh) > 10 cm) within a randomly laid 1000 m x 10 m belt transect. Lunney et al. (2000) sampled 20 x 20 m quadrats in which faecal pellet searches were conducted within a 1 m radius around the base of every tree; but a 1x1 m quadrat was also searched at a random location under the canopy of each identified tree within the larger quadrat (Lunney et al. 2000).

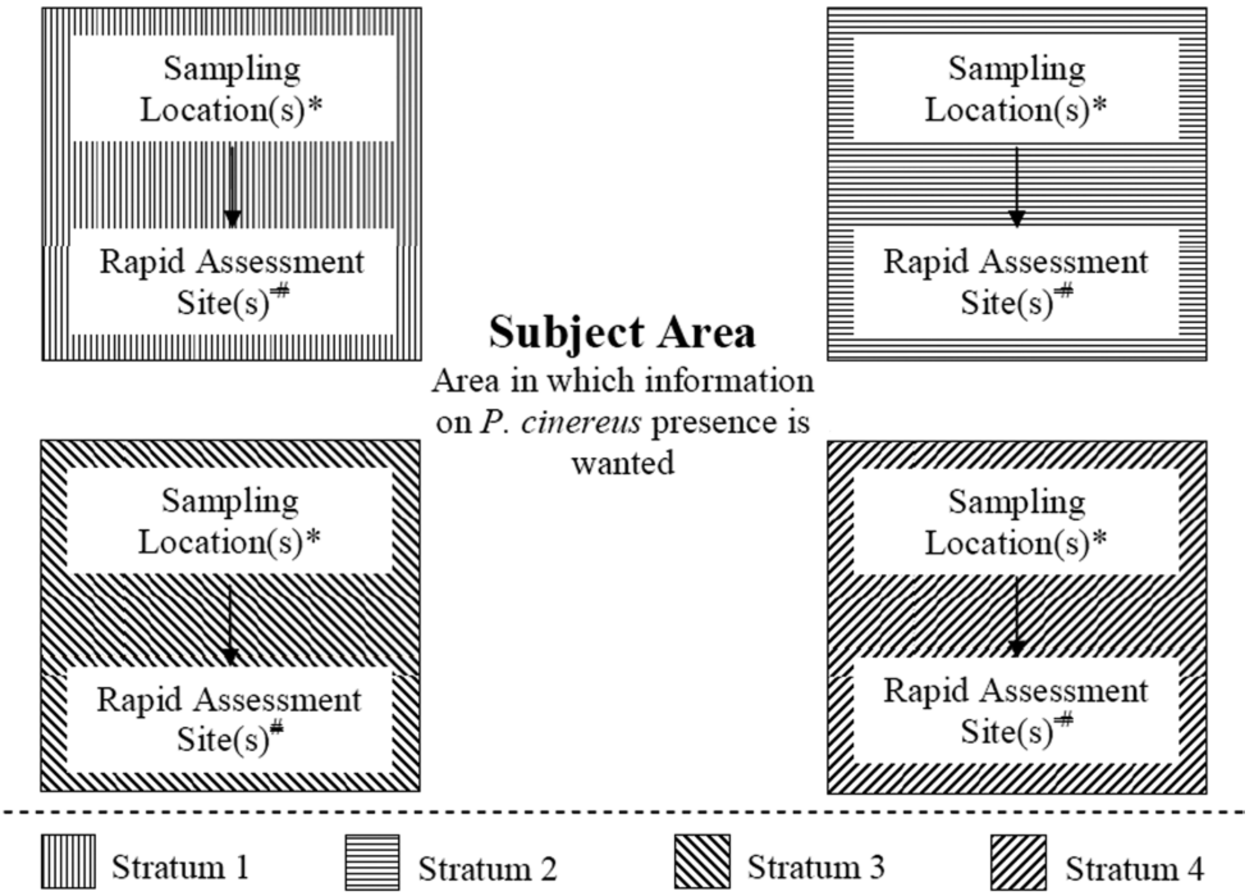
All the studies described above may have severely diminished the chances of detecting faecal pellets, though the additional randomly located quadrats used by Lunney et al. (2000) may have partly ameliorated the problem. Phillips & Callaghan's (2011) own analysis concludes that the odds of finding a pellet within 1m of the tree trunk is slightly less than tossing a coin and the data were derived from a single tree species at a single location. Whilst they correctly point out "faecal pellets were <u>not</u> uniformly distributed beneath the tree canopy" it would be overly simplistic to interpret their figures as indicating density of pellet deposition, since the pattern of deposition is far from uniform and their interpretation ignores the not uncommon situation that when *P. cinereus* defecate they do so whilst on lateral branches away from the trunk. Phillips & Callaghan (2011) correctly draw attention to "the problems of accumulated faecal pellet counts" and as their Figure 2 demonstrates, most pellets were located more than 1 m from the tree trunk. Ellis et al. (1998) studied the distribution of faecal pellets deposited under a variety of tree species in a variety of geographical locations; their finding that the faecal pellet recovery rate was only 18% within a 1 x 1 m area around the base of trees was broadly confirmed by Figure 2 in Phillips and Callaghan (2011), which indicates about 20% of pellets were located within a 0.5 m radius of the trunk. However, Ellis et al. (1998) observed that the pellet distribution did not follow a gradual radial pattern but was very patchy – as might be expected from trees of varying geometry and varying location of animals when they defecated.

Development of an optimised faecal pellet sampling protocol: the koala rapid assessment method (KRAM)

For indirect detection of *P. cinereus* presence to be valid, a standardised, robust approach is critical. Here we propose a generic protocol (refined to overcome significant errors in previous methods) for developing and employing a rapid assessment methodology to determine *P. cinereus* presence and then provide an example of the application of this methodology.

1. Selection of locations in which faecal pellet searches are to be conducted will normally incorporate stratification of the study area based on landscape scale features which are known to or are predicted to influence *P. cinereus* distribution. Within habitat strata (e.g. plant communities, underlying geology, elevation, slope, aspect, level of disturbance) discrete sampling locations must be randomly selected.
2. A pre-determined standardised sampling protocol must be consistently applied at each sampling location. Factors to be considered include the number of individual rapid assessment sites to be sampled at each sampling location (e.g. all trees in one quadrat, three sites along a 150-m transect, etc. – more than one rapid assessment site per sampling location is recommended); the sampling effort to be undertaken at each rapid assessment site (e.g. 30 person mins; 30 trees searched per site; all trees within quadrat); and the search effort per tree (e.g. around tree base and beneath canopy of tree).
3. A pre-determined protocol must also be applied to define the exact location of the rapid assessment site on the ground (e.g. systematically select the tree closest to the randomly generated GPS coordinate and search around that point; where this is not possible on the ground then make the GPS coordinate the northern-most point of the search; if that is not possible either, then make it the southern-most point; etc.).
4. Faecal pellet searches should begin at the base of the tree but not be limited to it.
5. Where temporal variability in habitat utilisation by *P. cinereus* has the potential to influence sampling results, or where faecal pellet persistence and / or detectability may be reduced due to site-specific factors (structure and micro-climate at ground layer: Sullivan et al. 2002, Rhodes et al. 2011), replication of the entire sampling program or increased sampling effort should be considered.

The habitat stratification and survey protocol is likely to need customisation based on the specific objectives of individual assessments. An overview of the general approach described above is presented in Figure 1, while a schematic rapid assessment methodology approach for an individual sampling location within the wider survey area is provided in Figure 2.



*Number of sampling locations within each stratum can be the same, or tailored if ***P. cinereus*** habitat utilisation / density predicted to differ between strata.
#Number of rapid assessment sites per sampling location dependent on protocol selected for study.

Figure 1. Koala rapid assessment method: overview of general approach

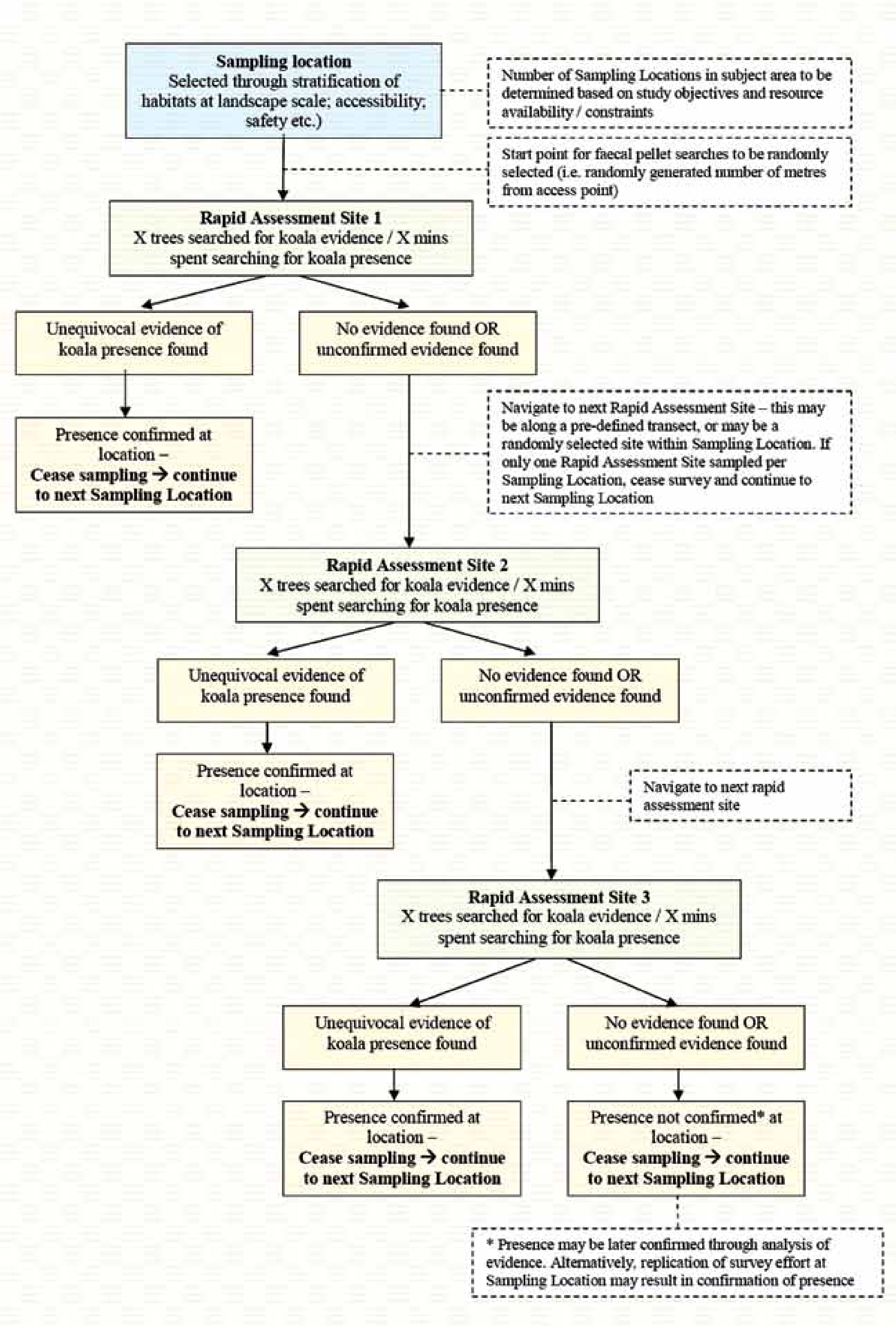


Figure 2. Koala rapid assessment method: schematic approach for an individual sampling location

Discussion

Benefits of the koala rapid assessment methodology KRAM

Two of the key elements that distinguish this method (KRAM) from the "spot assessment technique" (SAT) of Phillips and Callaghan (2011) are that (1) the selection of a rapid assessment site is not based on choosing a "focal tree", and (2) the search is not limited to a fixed radius around the base of trees. Indeed, in an unpublished preliminary study of *P. cinereus* on North Stradbroke Island (Woosnam-Merchez 2008) which used the KRAM, 60% of faecal pallets were detected under trees which are not conventionally expected to reveal evidence of *P. cinereus* usage; with the vegetation of some sites where faecal pellets were found being comprised only of such trees. With no previous records of observed *P. cinereus* or their pellets at most sites sampled in the preliminary survey of North Stradbroke Island, determining a "focal tree" would most likely have overlooked some habitats dominated by *Callitris sp.* or *Allocasuarina sp.*. Adoption of KRAM aims to reduce arbitrary preconceptions in order to minimise bias in *P. cinereus* presence / absence surveys.

While more detailed levels of investigation on *P. cinereus* ecology need to continue so as to develop a more comprehensive basis for understanding the species' biology, in applications where time and resources are constrained and knowledge of presence (and inferred absence – see below) is all that is necessary, the KRAM provides an effective and efficient means for acquisition of *P. cinereus* presence information. It should also be possible to use this method as the basis of 'area of occupancy' approaches to determining *P. cinereus* population trends, where the greater precision provided through determination of density estimates is not feasible.

For most populations the standard deviation of counts on sampling units rises linearly with density (Caughley and Sinclair 1994). Indeed, studies in the Koala Coast indicate that higher density sites require greater sampling intensity compared with low density sites to maintain a similar level of precision (Dique et al. 2001). In this context, the KRAM can provide an unbiased, preliminary indication of appropriate sampling intensity required in different strata for population estimate surveys. Using the KRAM as a tool to inform such surveys can significantly reduce the risk of under-sampling locations that could otherwise be undervalued as habitat for *P. cinereus* based on conventional expectations of what vegetation associations constitute habitat for the species i.e. forest or bushland not dominated by tree species that are conventionally considered to constitute habitat for *P. cinereus*. The random selection of sites within each stratum to be sampled, combined with the random selection of a start tree at each site (as opposed to selection of focal trees), removes a significant bias by providing data that are not based on preconceptions such as those inherent in the SAT.

Limitations of the KRAM protocol

Pellet detectability

Faecal pellet detectability can vary substantially on a site-by-site basis and this needs to be acknowledged when interpreting the results of a faecal pellet survey using the rapid assessment methodology or any other pellet search based method. Detectability is largely influenced by the structure, composition and complexity of the ground layer (Sullivan et al. 2002), as well as by pellet decay (Witt and Pahl 1995). Dense ground-layer vegetation, tall grass and accumulated debris (leaf litter, shed bark) all contribute to a reduction in faecal pellet detectability (Sullivan et al. 2002, Cristescu 2011). Issues of pellet decay are delicately modelled in work by Rhodes et al. (2011); however, their assumption of the species' pellet production rates at half the published values (they assume *P. cinereus* to produce some 80 pellets per day as opposed to the published figures of between 150 and 175: Ellis et al. 1998, Sullivan et al. 2004, Seabrook et al. 2011) throw into question the validity of their models. Rhodes et al. (2011) did not 'ground-truth' their modelled decay rates by reference to the observations of Witt and Pahl (1995) and the pellet production rates used in their model would have resulted in overestimating the number of *P. cinereus* individuals at their sites by a factor of two.

When using a standardised sampling protocol to find faecal pellets across a study area that supports a variety of vegetation communities, each is usually characterised by differing ground layer complexity. Hence the opportunity to detect faecal pellets through the implementation of the standardised protocol may not be consistent across the study area. This is particularly true if timed surveys are being undertaken – in sampling sites where pellet detectability is relatively high, more trees can be sampled per unit of time than at a sampling site where detectability is poor and thus a more intensive search effort at each tree is required. For this reason, it is proposed that if timed surveys (i.e. time spent searching each tree / time spent searching at a rapid assessment site) are performed, the amount of time dedicated should be proportional to the relative pellet detectability prevailing at the site (the poorer the detectability, the greater the survey effort required).

To overcome this potential limitation, it is recommended that for study areas which support a variety of vegetation communities and a high level of substrate heterogeneity (and which accordingly are likely to produce varying levels of pellet detectability) a survey protocol in which survey effort is strictly related to time spent searching should be avoided. Rather, search effort per tree should be related to relative pellet detectability, while search effort per rapid assessment site should be consistent across all sites within each individual sampling location and throughout the study area (e.g. 30 trees searched per rapid assessment site; all trees within X-m by X-m quadrat searched per rapid assessment site, see Cristescu 2011 for more details).

Inferring absence

While for many purposes, a single detection of presence is essentially an absolute finding and may be all that is required, failure to detect signs (i.e. faecal pellets) of *P. cinereus* use in an area is not conclusive. That is, absence of evidence is not evidence of absence. Failure to detect faecal pellets using the rapid assessment methodology may occur because:

- *P. cinereus* do not occur at the location (i.e. true absence);
- *P. cinereus* occur at the location, however, no faecal pellets were deposited at the sampled rapid assessment sites; or
- *P. cinereus* occur at the location, however, faecal pellets were not detected during the assessment because:
  - faecal pellets were not present under trees surveyed but were present under other trees in the area which were not examined;
  - pellets were deposited at the sampled sites but faecal pellets were not detected under trees when in fact present;
  - faecal pellets were deposited at the sampled sites but had decomposed before being found [decay rates depend on exposure to sunlight, moisture, invertebrate activities (Witt and Pahl 1995, Cristescu 2011, Rhodes et al. 2011)]; or
  - the faecal pellets were dispersed or obscured by exceptional physical disturbance of ground layer e.g. flooding, fire, etc.

Whilst determination of species' absence is problematic in all but the simplest communities, likely absence of *P. cinereus* from a location can be inferred based on results obtained from employing KRAM sequentially. It is proposed that absence only be inferred after sufficient replication of field studies using the rapid assessment methodology, such that potential temporal variability in habitat utilisation can be accounted for. For example, inferred absence might be claimed for a particular sampling location / study area if four visits at three monthly intervals fail to return any evidence of utilisation of that habitat by *P. cinereus*.

The KRAM approach provides a simple, reproducible method by which *P. cinereus* presence can be confirmed. To obtain additional information (i.e. determine dietary preference, value ranking of *P. cinereus* habitat or abundance estimates), additional survey effort is required. Specifically with respect to abundance estimates, KRAM should be used to inform the design of larger census surveys using an accepted technique (i.e. appropriate transect or other direct census methodology for calculating abundance) such as employed for the Koala Coast surveys (DERM 2012). While it is recognised that there may be a relationship between pellet occurrence and *P. cinereus* density (Dique et al. 2003, Sullivan et al. 2003b), using *P. cinereus* pellet frequency alone to estimate abundance is problematic without site specific establishment of parameters such as pellet detectability and persistence (Rhodes et al. 2011) and specific calibration of the relationship between pellet density and *P. cinereus* density (Sullivan et al. 2002, Dique et al. 2004). Reliable criteria for pellet aging in the context of individual sites also need to be developed (e.g. Witt and Pahl 1995). What is certain about finding *P. cinereus* pellets in the field is that an individual *P. cinereus* has previously been in the vicinity, but further inferences are unwarranted without further data.

Conclusion

A rapid assessment methodology based on detecting faecal pellets has the potential to be a valuable tool for the identification of *P. cinereus* presence. The KRAM approach enables identification of which habitats show evidence of *P. cinereus* utilisation so as to evaluate current distribution patterns, 'ground-truth' predictive mapping or inform the survey design for more detailed *P. cinereus* population surveys. Herein lies the principal value of the methodology – it provides a simple, non-invasive, reproducible technique for detecting *P. cinereus* presence and distribution at large spatial scales, which in turn can inform the development of more detailed studies such as population censuses and habitat mapping.

The key advantages of the approach include:

- It enables a time and resource efficient assessment of a fundamental aspect of *P. cinereus* ecology (i.e. distribution based on presence), that requires little advanced training;
- It does not rely on direct observation of *P. cinereus*, which is notoriously difficult, particularly where populations occur at low densities;
- Its site selection method reduces bias inherent in earlier pellet search protocols;
- It exploits the facts that faecal pellets are relatively easy to find on many substrates and are readily identifiable;
- It allows for an assessment of *P. cinereus* distribution to be undertaken over large spatial scales; and
- It is non-invasive.

The koala rapid assessment method (KRAM), when undertaken in association with supplementary objective criteria, can allow for likely absence to be inferred. Such data can contribute significantly to processes which require information relating to *P. cinereus* presence / absence, including land use planning, development assessment and impact mitigation. Furthermore, KRAM can contribute to *P. cinereus* conservation efforts through the provision of data to inform the design of population census and habitat mapping studies; as well as to 'ground-truth' predictive mapping of *P. cinereus* habitat.

Care must be taken not to over interpret data obtained using methods that sample for *P. cinereus* faecal pellets. While KRAM is unable to reveal much more about *P. cinereus* ecology other than presence / absence, when applied in a standardised and rigorous manner, the technique is certainly worth having in the ecological tool box since it overcomes the principal flaws inherent in some other previously described *P. cinereus* faecal pellet detection methods (such as SAT - Phillips and Callaghan 2011) whilst being less resource intensive than pellet based abundance estimation methods (e.g. Sullivan et al. 2004).

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